

## ELICITATION OF BROWN TREESNAKE PREDATORY BEHAVIOR USING POLYMODAL STIMULI

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**Abstract:** The brown treesnake (*Boiga irregularis*) is a species of special management concern, requiring improvement of capture methods through the development of effective artificial lures. Toward this end, we used night-vision cameras and mechanical models to study the interplay of sensory modalities for stimulating predatory behavior in brown treesnakes. Snakes oriented toward live mouse (*Mus musculus*) lures in complete darkness as much as they did to live mice lures under visible-light illumination; however, brown treesnakes in an unlighted environment responded qualitatively differently by probing and biting at the lure holder rather than striking at the mouse within (as did snakes in lighted trials). We altered the odors and vibratory cues of mechanical models to partition attractive stimuli and to measure snake response to vibratory cues. Fur-covered odorized (by rubbing with freshly defrosted dead neonatal mouse) models were more attractive than fur-covered non-odorized models, odor alone, and empty lure holders. Brown treesnake response to live mice did not differ from their response to smooth, odorized models, and moving versions of the smooth, odorized models stimulated more predatory behavior than unmoving models. Response from brown treesnakes appears to increase as odor and mechanical vibration stimuli are increased quantitatively and/or qualitatively. Conceptually, we hypothesize that polymodal stimuli synergize to promote predatory behavior in foraging snakes and that for trapping purposes, a multi-sensory attractant, optimized at each modality will be required to achieve capture success similar to or better than that obtained using live mice lures.

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The brown treesnake is a nocturnal Australasian colubrid with an ontogenetically shifting catholic diet that includes live and dead prey (Savidge 1987, 1988; Chiszar 1990; Rodda 1992; Shivik and Clark 1999a). The snake is a primary management concern because it has caused the decline and extinction of avifauna and herpetofauna, numerous power outages, the loss of domestic animals, and is likely to be transported elsewhere (Fritts et al. 1987, Savidge 1987, McCoid 1991, Fritts and McCoid 1991, Rodda and Fritts 1992). The U.S. Department of Agriculture has implemented a containment and

monitoring program in areas, i.e., cargo and military facilities, where snakes have a high likelihood in being transported from Guam (U.S. Department of Agriculture 1996). Traps are the most intensively used management tool (M. E. Pitzler, Wildlife Services, Guam, personal communication), but maintenance of live mice attractants requires animal care that is labor intensive and expensive. An effective inanimate attractant is required, but its development is dependent upon an understanding of the predatory behavior of brown treesnakes.

For snakes, the importance of individual sensory modalities for stimulating predatory behaviors varies. For example, *Crotalus* and *Tham-*

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nophis may require genetically programmed (Arnold 1981, Burghardt 1971, Burghardt et al. 1988) chemical cues to elicit attack behaviors (Halpern and Frumin 1979, Wilde 1938). Various researchers have studied brown treesnake response to odor cues (Chiszar et al. 1993, 1997a; Shivik and Clark 1999b), and visual cues (Chiszar et al. 1988). Different sensory modalities interact, possibly synergistically (Shivik 1998), because the absence of a salient visual cue lessens brown treesnake interest in chemical cues (Chiszar 1990). Odor cues are clearly important for brown treesnakes as well, because they will enter traps baited only with bird odors (Fritts et al. 1989), and blindfolded brown treesnakes can efficiently attack and kill prey (Kardong and Smith 1991), but it is likely that an effective attractant will require both visual and chemical components (Chiszar et al. 1997b).

The construction of an effective inanimate lure requires intensive research because the relative importance of sensory cues is dependent upon both the variety and quality of cues presented (Shivik 1998, Shivik and Clark 1997) as well as seasonal and environmental factors (Rodda et al. 1999a, Shivik et al. 2000). Further analysis of this species' predatory behaviors is required to complete our understanding of variability in brown treesnake response to prey stimuli.

Previous researchers used simple mechanical models to stimulate predatory behavior in brown treesnakes (Lindberg et al. 2000, Shivik 1999); therefore, we designed more complex models for use in experiments. The use of models for studying animal response is a common method in ethology and as with any research tool, models should be used with caution (Lehner 1996), but mechanical models allow controlled studies identifying the combination of the sensory stimuli that will best heighten appetitive behavior in foraging snakes. Our objective was to investigate predatory behavior of brown treesnakes with the goal of providing information that will assist in the development of effective inanimate attractants for them; specifically, we employed mechanical models to study the predatory response of brown treesnakes to combinations of animate (i.e., alive), inanimate, movement, and odor stimuli.

## METHODS

We performed a linear progression of individual experiments to identify stimuli that pro-

moted predatory behavior. To monitor snake response to stimuli, we used video recordings of captive brown treesnakes on Guam. Using the tapes, we measured the amount of time snakes oriented toward the lure (i.e., probed, bit, and struck at a lure), investigated (probed other areas of the cage), and rested (coiled and unmoving). For the measure of predatory behavior, we used the proportion of time orienting as the dependent variable. Experiments were performed on Guam during November of 1998 and May of 1999.

In all studies, recently wild-caught snakes (in captivity <4 weeks) on Guam were used as experimental subjects, and individual snakes were not used more than once in any 1 experiment. Captured snakes were allowed to acclimate in their individual holding cages (33 × 24 × 24-cm tubs) for >2 days before testing. Trials were run between 0400 and 1100 hr to limit study to a normal time of snake activity (Fritts et al. 1987). During each 1-hr trial, lures were placed into a hardware cloth container (7 × 7 × 20 cm box), and put in the snake's cage. Cages had a clear plastic cover to allow video taping of snake behavior. Unless otherwise noted, we used ANOVA to detect differences between conditions, checked assumptions using residual plots, and used the Tukey method of multiple comparisons (SYSTAT 5.04, SYSTAT Evanston, Illinois, USA).

## Lighted vs. Unlighted Trials

During 20–25 May 1999, we used live mice lures to compare snake response to an animate lure under fully illuminated or completely dark conditions. Unlighted conditions were produced by running trials under a suspended tarp in a darkened room in an unlighted warehouse at night. Behaviors were recorded using commercially available (Sony TR-416) night-vision (i.e., sensitivity to infrared wavelengths emitted from their infrared lamps) video cameras.

## Movement, Odor, and Textured Models

During 2–23 November 1998, we studied several forms of mechanical models to identify combinations of sensory cues that were attractive to brown treesnakes. Models were constructed using a 5.5-cm-long, 2.5-cm-diameter white PVC pipe in which was tightly fitted a DC hobby motor (Cer Bag Motor FA 130). The device was made to wobble when activated by attaching an unevenly weighted fly-wheel to the

shaft of the motor. A timer circuit turned the device on for a 13-sec activation period and off for a 33-sec deactivated mode. To observe individual and combined effects of polymodal stimuli, we defined experimental treatments by adding odor and visual stimuli incrementally. The treatments tested were an empty lure chamber (control; C), odor (freshly defrosted neonatal mouse obscured in black felt; O), smooth moving model (SMM), a furry (artificial fur-covered) moving model (FMM), an artificial fur-covered moving model presented simultaneously with a mouse odor (FMMO), and a live mouse (LM). We hypothesized that brown treesnake interest in the models would follow an increasing trend as sensory cues were added:  $C < O < SMM < FMM < FMMO < LM$ .

### Movement, Odor, and Quiescent Models

Because neither an unmoving odorized model (a movement control) nor a smooth, odorized moving model were used in the first series of mechanical model trials, we performed a second series of trials (May 1999) to determine the attractiveness of other stimulus combinations compared to a live mouse control. An odorized moving model (MMO) was created by rubbing a freshly defrosted mouse on the moving model, and snake response to this treatment was compared with response to a non-moving identically odorized model (MO) and to a live mouse.

### Movement Cycle

Initial models were built with 1 movement cycle (28% active, 68% inactive, 46-sec cycle). However, the amount of movement (percent of time vibrating compared to time quiescent) could affect the predatory behavior in brown treesnakes. Therefore, we designed mechanical models that could be adjusted in periodicity. Cycle length for the adjustable cycle model was 65 sec, but the period of activity was varied between constant movement, medium movement (50% active duty cycle), low movement (35% active duty cycle), and zero movement. Motors were housed in 4.0-cm  $\times$  2.0-cm plastic tubes and covered with a thin layer of adhesive backed blister-relief (moleskin) fabric to provide a substrate on which to apply mouse odor. Experiments were performed during May 1999 and all models were odorized by rubbing with a freshly defrosted dead neonatal mouse. A live mouse served as a positive control.

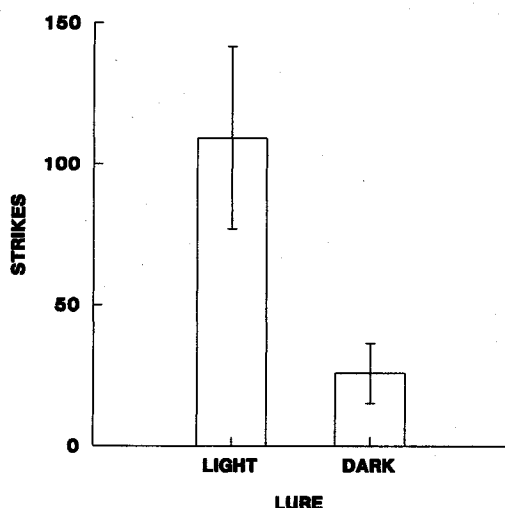


Fig. 1. Relative number of strikes brown treesnakes made at live mice in lure holders under room-light ( $n = 11$ ) or dark ( $n = 15$ ) conditions during trials on Andersen Air Force Base, Guam during May, 1999. Bars represent 1 SE.

## RESULTS

### Lighted vs. Unlighted Trials

Eleven snakes were observed under light conditions and fifteen were tested under dark conditions. We did not detect a difference in the proportion of time snakes spent orienting to live mouse prey, whether or not mice were presented in light or complete darkness ( $\bar{x} = 0.778$  and  $\bar{x} = 0.775$ , respectively;  $t_{24} = 0.03$ ;  $P = 0.98$ ). However, while reviewing the video tapes of trials, we noted an obvious difference in snake behavior depending upon whether prey were presented in lighted or dark conditions. Snakes with illuminated lures appeared to be more active, striking at the mouse rather than only probing and biting at the mouse holder. We reexamined these video tapes, recording the number of strikes snakes made at the mouse. Snakes in light conditions frequently struck at mice ( $\bar{x} = 109.2$  strikes/trial) and the snakes in darkness mostly probed and bit at the mouse-holding chamber while striking less ( $\bar{x} = 27.5$ ;  $t = 3.40$ ,  $P = 0.002$ ; Fig. 1).

### Movement, Odor, and Textured Models

As stimuli were added to attractant models, brown treesnakes spent more time orienting toward the models ( $P < 0.001$ ; Fig. 2). Response to LM ( $n = 11$ ) was the greatest, and live mice promoted more predatory behavior than FMM ( $n = 12$ ), MM ( $n = 10$ ), O ( $n = 11$ ) and C ( $n$

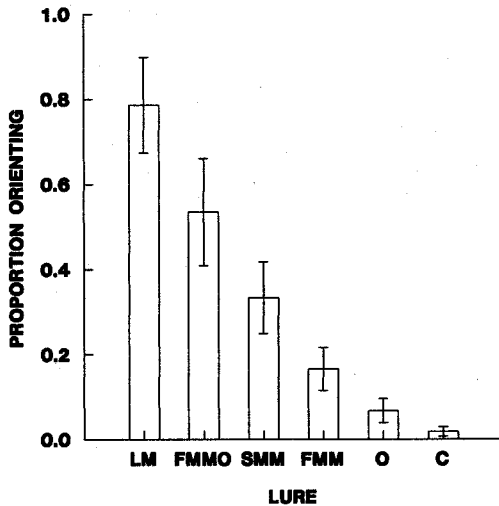


Fig. 2. Proportion of time captive brown treesnakes spent orienting toward live mice (LM), an artificial fur-covered moving model with odor from a freshly defrosted mouse (FMMO), a smooth moving model (SMM), a fur-covered moving model (FMM), a mouse odor (O), or an empty, control lure chamber (C) in trials on Andersen Air Force Base, Guam during November 1998. Bars represent 1 SE.

= 12;  $P < 0.002$ ). Fur-covered moving models with mouse odor ( $n = 10$ ) elicited more predatory behavior than models without odor, FMMO > FMM ( $P = 0.015$ ), and were also more attractive than the control ( $P = 0.001$ ). Response to fur-covered moving models with odor was greater than the odor-only treatment (FMMO > O;  $P = 0.001$ ).

### Movement, Odor, and Quiescent Models

We were not able to statistically distinguish differential response from brown treesnakes toward live mice ( $n = 11$ ) and mechanical, odorized models ( $n = 13$ ;  $P > 0.99$ ; Fig. 3). However, both mice and an odorized moving model stimulated more predatory behavior in brown treesnakes than an unmoving, odorized model ( $n = 11$ ;  $P = 0.02$ ).

### Movement Cycle

Captive brown treesnakes responded to live (LM,  $n = 12$ ) and inanimate (constant,  $n = 11$ ; medium,  $n = 10$ ; low,  $n = 10$ ; zero,  $n = 12$ ) lures differently ( $P < 0.001$ ). The snakes were stimulated most by live mouse lures (LM > Constant, Medium, Low, and Zero movement;  $P < 0.009$ ). However, among the inanimate attractants, constant movement was more attractive than Low ( $P = 0.07$ ) and Zero movement ( $P = 0.005$ ; Fig. 4).

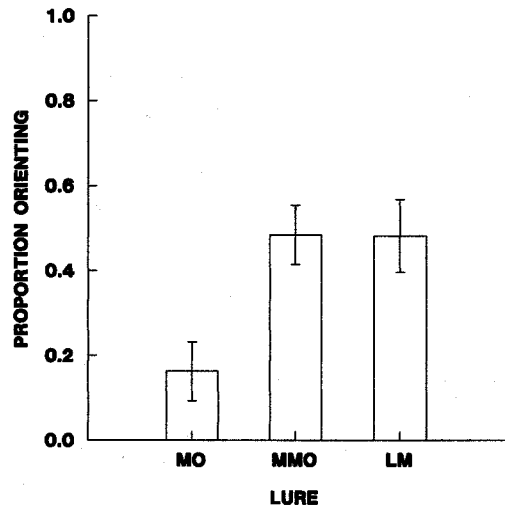


Fig. 3. Proportion of time captive brown treesnakes spent orienting toward live mice, moving models, and mouse odors in trials on Andersen Air Force base, Guam during May 1999. MO = model odorized by rubbing with a freshly defrosted mouse, MMO = moving model odorized with a live mouse, LM = live mouse. Bars represent 1 SE.

## DISCUSSION

We cannot rule out brown treesnake sensitivity to the sub-visible light wavelengths used by our night vision cameras, but given the differences in behavior observed in the trials, we believe that our snakes could not see the mouse

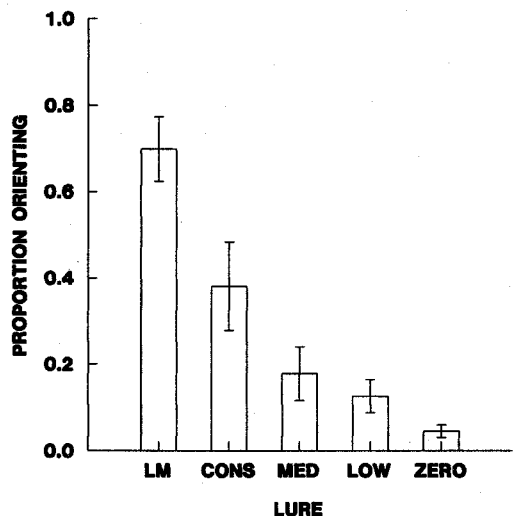


Fig. 4. Proportion of time captive brown treesnakes spent orienting toward attractants of varying activity level during trials on Andersen Air Force Base, Guam during May 1999. LM = live mouse, CONS = constant movement, MED = 50% on/off, LOW = 35% on cycle, ZERO = no movements. To produce mouse odor, models were rubbed with freshly defrosted mice. Bars represent 1 SE.

lures in unlighted conditions. Our results replicate and confirm work done by Kardong and Smith (1991), but of significance in this study is our determination that the quantity of predatory behavior was not altered with darkness, but that the quality and form of predatory behavior was. With a complete polymodal picture of mouse prey, snakes shifted from the seek sequence of appetitive behavior to the attack and consume mode; they struck repeatedly and directly at mouse lures. When presented with an incomplete sensory picture, snakes maintained heightened search and probe behaviors, but rarely struck at the mouse prey.

Anecdotally, during our observations of brown treesnake behavior we noted occasions when snakes in complete darkness appeared to track the mouse as it moved from one end of its chamber to another. We observed an instance when a snake in darkness was orienting toward a mouse, then the mouse moved to the other end of its chamber, and after a short lag (2–3 sec) the snake reoriented its head again toward the mouse, suggesting some ability to locate prey using thermal or vibratory cues. We did not design experiments to measure thermal acuity, nor were we able to separate out the ability of brown treesnakes to use vibratory cues to determine mouse position, but believe that future experiments should more thoroughly investigate the sensory capabilities of these snakes.

The trend in attractiveness (Fig. 2) was interesting because adding fur to a moving model did not directly result in attraction higher than the uncovered moving model. Data suggested that the smooth model may be more attractive than a fur-covered one (Fig. 3), and we believe that this effect may be because of the tendency of fur covering to dampen the vibrations of our mechanical models. That is, the effects of the fur-covering were confounded with possible effects of movement amplitude in these trials, and further research should attempt to more thoroughly understand the effect of vibratory amplitude on snake response. Also, it is tempting to state that a smooth, moving, odorized model is as effective as live mice for attracting brown treesnakes (Fig. 3), but based on lower snake response to similar models (Fig. 4) and the limitations of laboratory trials, thorough field testing of lures is required before accepting the hypothesis of equivalent attraction to live mice and this artificial lure.

We noted responses of brown treesnakes to artificial models. With moving lures, we measured an increase of predatory behavior, especially the types of actions that would result in a snake being caught in a trap, but snakes appeared to respond to odor and vibratory cues, and not necessarily to the source of the cues. That is, although their predatory behaviors intensified, snakes did not always appear to identify the moving model as a potential food item. With artificial lures, snakes probed at the lure chamber like they probed at live mice lure chambers in darkness, but the model itself was rarely struck at and did not appear to be the object of attention, even though it was the object providing odor and vibratory cues. An effective artificial lure may need to focus, and not only stimulate, brown treesnake predatory behavior (which our models did not appear to do effectively).

Movement is clearly a stimulant of brown treesnake appetitive behavior, and this paper may merely formalize common knowledge of herpetoculturists and the general public: wiggling dead mice tends to promote feeding by captive animals (Larson 1989:216). However, more intensive study is required to elucidate the influence of the actual look of prey, e.g., fur covering, legs, eyes, or shape, on brown treesnake foraging, and the types of appetitive and predatory behaviors that result in trap capture.

The combination of the best movement and odor cues may result in a polymodal suite of artificial stimuli that is more attractive to brown treesnakes than a natural mouse lure. For instance, mice are not active constantly through the night and if artificial movement is attractive to snakes, it follows that intense and frequent artificial movement throughout the night may be more attractive than intermittent movement from live mice. By altering periodicity and amplitude of mechanical lures, an attractive visual and vibratory cue may be developed. Similarly, continued investigation of the odors of dead mice is likely to identify the attractive components of this odor, which is sometimes as attractive as live mouse odor (Shivik and Clark 1997). However, there will be a physiological limit to the response of an animal to any stimulus, and more of a stimulus does not necessarily promote increased response.

The differential behavioral response of brown tree snakes to chemical or visual lures has interesting implications for the design of trapping

lures. The effectiveness of brown treesnake traps varies with environmental conditions such as wind and rain (Shivik et al. 2000, Rodda et al. 1999a), but causative factors for variability in trap success may be due to behavioral and other conditions. For a brown treesnake to be captured in a standard trap (Linnell et al. 1998, Rodda et al. 1999b), the snake must probe the surface of the trap until it pushes through a 1-way door flap. Thus, probing and investigatory behaviors, and not active striking, should result in brown treesnakes being captured in traps. Hypothetically, such behaviors may be more likely to occur when traps and mouse lures are placed in dark forest interiors or on moonless nights.

Brown treesnakes can hunt in complete darkness, and the quantity and quality of appetitive response varies directly with the variety, intensity, and quality of prey-like polymodal stimuli presented. As such, brown treesnakes probably do not form a singularly visual or chemical search image for prey recognition. The snakes, when receiving polymodal cues, heighten their responses accordingly by adding cues together rather than by relying on a particular sensory modality. Therefore, the concept of switching from a preferred sensory modality to a less preferred one (Chiszar 1990) is useful in the context of understanding the capabilities of brown treesnakes, but limited as a theoretical framework describing brown treesnake response to multi-sensory cues. For lure construction, a more appropriate theoretical context may be to interpret data in an additive and classical sense, noting that the addition of cues (i.e., individual releasers) results in a synergistic intensification of brown treesnake predatory behavior. If a prey item search image is formed, it is likely to be polymodal; when all sensory aspects of the cue are apparent, intense predatory behavior results.

## MANAGEMENT IMPLICATIONS

A combination of sensory cues is likely to be required for an attractant to be effective (Chiszar 1997). Brown treesnakes show some interest in odor cues, but not at the level required to result in high capture rates using standard traps. We believe that managers should continue investigations of alternative attractants, but based on the effort required to produce polymodal stimuli using battery-operated models, we acknowledge that it may be easier to develop al-

ternative trap designs (e.g., door-less traps with adhesive substrates) than to develop a more attractive attractant. Alternative trap designs should reduce the difficulty of the behavioral task of entering a trap rather than rely on the development of a complex polymodal attractant.

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